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Perspective

Linking Forest Flammability and Plant Vulnerability to Drought

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Received: 10 June 2020; Accepted: 16 July 2020; Published: 20 July 2020

Abstract: Globally, fire regimes are being altered by changing climatic conditions. New fire regimes have the potential to drive species extinctions and cause ecosystem state changes, with a range of consequences for ecosystem services. Despite the co-occurrence of forest fires with drought, current approaches to modelling flammability largely overlook the large body of research into plant vulnerability to drought. Here, we outline the mechanisms through which plant responses to drought may affect forest flammability, specifically fuel moisture and the ratio of dead to live fuels. We present a framework for modelling live fuel moisture content (moisture content of foliage and twigs) from soil water content and plant traits, including rooting patterns and leaf traits such as the turgor loss point, osmotic potential, elasticity and leaf mass per area. We also present evidence that physiological drought stress may contribute to previously observed fuel moisture thresholds in south-eastern Australia. Of particular relevance is leaf cavitation and subsequent shedding, which transforms live fuels into dead fuels, which are drier, and thus easier to ignite. We suggest that capitalising on drought research to inform wildfire research presents a major opportunity to develop new insights into wildfires, and new predictive models of seasonal fuel dynamics.

Keywords: drought; flammability; fuel moisture; leaf water potential; plant traits; wildfire

1. Introduction

Fire has played an important role in determining the composition and distribution of ecosystems almost since the emergence of the first land plants [1]. In many regions, the frequency of wildfires is projected to increase under climate change due to changes in fuel (i.e., biomass) production, accelerated aboveground biomass turnover rates and fuel drying [2]. This increase in wildfire frequency has the potential to drive species extinctions and cause ecosystem state changes [2]. Indeed, conversion of forests to shrublands or grasslands due to increased fire frequency is already occurring in the Mediterranean Basin [3], the western United States [4] and south-eastern Australia [5]. The role of wildfires in the terrestrial carbon cycle [6], and subsequent feedbacks into the climate system, as well

as potential implications for precipitation [7], highlight an urgent need to increase our understanding of the climate–fire–vegetation interactions underlying global fire regimes. At the same time, predicting the likelihood of wildfire at shorter time scales (weeks–months) is required for land managers to target suppression resources in order to protect people, property and infrastructure, as well as fire-sensitive ecosystems.

Large fires generally coincide with periods of high soil water deficit and atmospheric water demand in most forests and woodlands [8]. In these ecosystems, spatially continuous arrays of fuel (e.g., litter, foliage, twigs) are usually present, except for immediately after fire. However, these fuels are usually too wet to propagate fire. During drought or seasonal dryness, the moisture content of these fuels declines [8,9]. Low fuel moisture content increases the probability of ignition, rate of fire spread and fire intensity [10–12]. While low fuel moisture content is likely to be important for the probability of ignition and initial rate of spread, other factors such as fuel load, wind and terrain can be of greater importance for subsequent fire behaviour [13]. Thus, dry fuels are a prerequisite for large forest fires, along with weather and ignition sources ([14]; Figure 1).

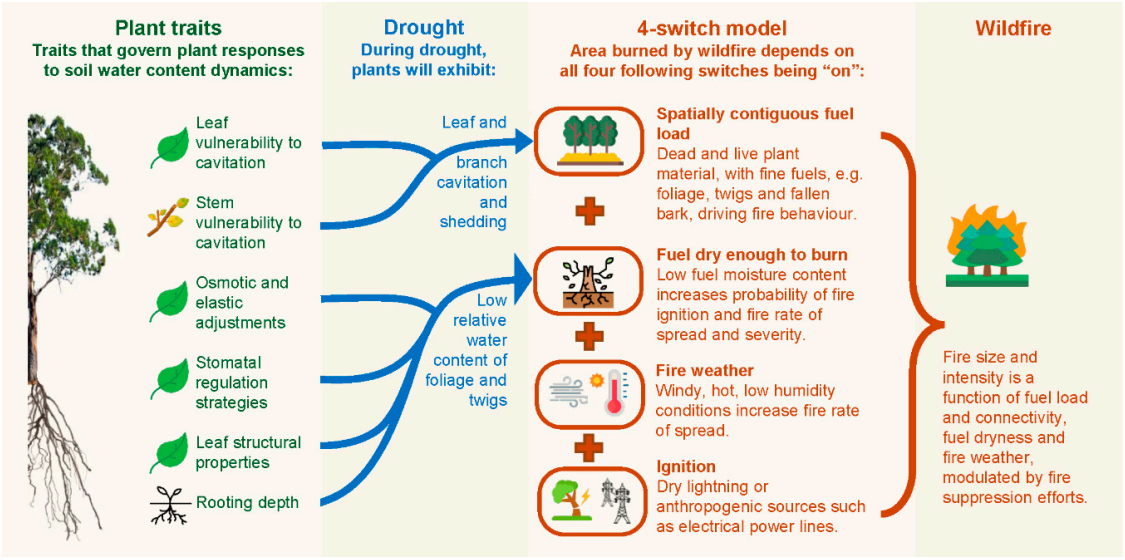

Figure 1. Conceptual model illustrating linkages between drought-related plant traits and the likelihood of wildfire. The 4-switch model is outlined in Bradstock [14].

In addition to causing declines in fuel moisture content, drought or seasonal dryness can also cause changes in the ratio of dead to live fuels [15,16]. Drought stress and subsequent mortality is potentially an important mechanism driving large wildfires, since the moisture content of dead fuels can decline far below that of live fuels (e.g., ~7–30% for dead fuels and ~50–200% for live fuels; [9]). For example, following drought-induced dieback in the Jarrah forests of south-western Australia, Ruthrof et al. [15] observed a large increase in surface fine fuel loads (i.e., litter). Additionally, tree mortality was associated with a more open canopy, which affected the microclimate of the forest floor, increasing temperature and vapour pressure deficit, and hence the rate of drying of the understory and litter fuels [15]. These changes in forest structure resulted in a 30% increase in predicted fire spread rates [15]. Thus, drought events can increase the probability of wildfire through multiple mechanisms, including changes to understory microclimate, fuel moisture, forest structure, the ratio of dead to live fuels in the canopy, and the amount of litter on the forest floor.

As drought events become more severe, there is increasing attention being paid to drought-induced tree mortality. This concern is driving a wave of research into plant vulnerability to drought and plant water relations under stress [17,18]. However, despite the co-occurrence of forest fires and drought, and recognition of the role of plant physiology and phenology in governing the moisture content of

live fuels [8], current approaches to modelling fuel attributes, such as live fuel moisture content or the ratio of dead to live fuels (i.e., foliage), generally do not explicitly incorporate plant physiological responses to water stress (but see [19–22]).

There is a tremendous opportunity to capitalise on recent advances in drought research to inform our understanding and prediction of fuel attributes such as live fuel moisture content and dead:live fuel ratios. Currently, live fuel moisture content (LFMC, moisture content of foliage and twigs) is monitored through satellite remote sensing (e.g., [9,23]) or inferred from drought indices that require species-specific calibrations (e.g., [24,25]). However, remote sensing can at best only estimate LFMC in near real-time, and cannot be used to predict flammability under future (novel) climatic conditions. Drought indices lack the physical basis required to reliably quantify flammability outside of the ecosystems for which they were calibrated. Similarly, while there is recognition of the importance of dead to live fuel ratios on fire behaviour [26,27], these ratios are currently only inferred from drought indices (e.g., in the United States National Fire Danger Rating System, [28]), if at all.

Here, we demonstrate how drought-related research can be used to advance our understanding of forest flammability. We use the term "flammability" to refer to the general ability of vegetation to burn, following Gill and Zylstra [29]. We particularly focus on the potential applications of drought-related research to inform the prediction of live fuel moisture content and changes to the ratio of dead to live fuels in the forest canopy. These fuel attributes are fundamentally important constraints of wildfire [14,30,31] and underpin many fire behaviour models for forests. For example, many of the fire behaviour models used in Australia and North America require inputs of fuel load, particularly of surface fuels (i.e., litter) and fuel moisture content, which is often approximated by drought indices [32,33]. Here, we (i) present a conceptual model illustrating the links between plant responses to drought and critical fuel properties limiting the probability of landscape-scale fire (specifically live fuel moisture content and dead: live fuel ratios); (ii) demonstrate that established relationships between leaf water content and leaf water potential (pressure-volume curves) can be adapted to model live fuel moisture content; (iii) present a framework for modelling live fuel moisture content from soil water content and drought-related plant traits; and (iv) examine potential links between physiological drought stress, including leaf cavitation and shedding, and fuel attributes. We do this via a combination of literature review and analyses from a common garden experiment presented here as a case study. Our goal is to stimulate joint research on plant responses to drought and forest flammability.

2. Linking Fire with Drought: A Conceptual Model

For landscape-scale fires to occur, four conditions need to be met: (i) the presence of spatially contiguous fuel; (ii) that fuel being dry enough to burn; (iii) weather conditions favourable to the spread of fire; and (iv) an ignition source (e.g., lightning; [14]). These conditions have been characterised as switches, with all four needing to be activated for wildfires to occur ([14]; Figure 1). We posit that the second switch (fuel dryness) is influenced by plant responses to drought, which in turn are governed by plant traits (Figure 1). The first switch (fuel load) is also likely affected, to some extent, by plant responses to drought (Figure 1). For live fuels, moisture content is a function of soil water availability across the root zone, and the osmotic and elastic adjustments that determine the relationship between leaf water content and leaf water potential [34]. Moisture content is also a function of leaf structural properties, which set the limit on maximum water content [35].

For fuel load, we suggest that both the quantity and spatial arrangement are modified by drought-related plant traits. For example, during extreme drought which results in canopy dieback, there may be a large, temporary transformation of live fuels into dead fuels. When this senescing foliage is finally shed from plants, the density of live fuels in the canopy will decrease. At the same time, the influx of litter into the surface fuel layer will be relatively uncompacted, and thus well-aerated, and therefore more readily available to burn [36]. These relationships between plant responses to drought and fuel properties are conceptualised in Figure 1. We now explore these linkages between plant responses to drought and forest flammability in detail.

3. Common Garden Case Study

We use a common garden experiment as a case study to examine the hypothesised linkages between drought-related plant traits and wildfire risk outlined in Figure 1. Eight *Eucalyptus* tree species originating from across a strong gradient in rainfall (250–1125 mm), temperature (10–21 °C) and moisture index (0.2–1.1; ratio of mean annual precipitation to potential evapotranspiration) across New South Wales, Australia, were grown in a common garden. The eucalypts were sourced from a range of vegetation communities (wet sclerophyll forest, dry sclerophyll forest, grassy woodland and semiarid woodland). Further details of the study design and data were provided in Li et al. [37], Li et al. [38] and Blackman et al. [39]. Images of the leaves of each species are provided in Figure S1. Saplings of the eight eucalypt species were progressively dried and coupled measurements of leaf water potential (Ψ_{leaf}) and live fuel moisture content (LFMC) of foliage were taken periodically at pre-dawn and midday during the imposed drought. Measurements were undertaken on >56 leaves per species and >7 individuals per species. During the drought, the canopy leaf area that each plant lost progressively to leaf shedding was calculated from measurements of the dry weight of shed leaves and the mean leaf mass per area (LMA) of foliage sampled prior to the drought treatment. For each species, the Ψ_{leaf} value associated with initiation of leaf shedding was calculated by averaging Ψ_{leaf} values when some leaf shedding had occurred but >90% of the plant leaf area was still present. Leaf hydraulic vulnerability to drought-induced embolism was also measured (see [38]).

4. From Relative Water Content to Live Fuel Moisture Content

The foundation of the linkage between drought and fire is the moisture content of fine fuels (e.g., foliage, twigs). In the drought literature, the water content of foliage is characterised as relative water content (RWC), whereas in the fire literature it is characterised as live fuel moisture content (LFMC). However, these metrics are two sides of the same coin. Both RWC and LFMC quantify the mass of water in foliage, with RWC expressing this mass relative to saturated water content, whereas LFMC expresses this mass relative to foliar dry weight (Equations (1) and (2), respectively). The similarity of these two metrics means that the response of LFMC to drying soils can be modelled in the exact same way that RWC is modelled. In the drought literature, RWC is commonly modelled as a function of leaf water potential (Ψ_{leaf}). This relationship is characterised by the pressure–volume curve [34], which is a fundamental method of assessing drought tolerance [40].

$$\text{RWC} = \left(\frac{F_w - D_w}{T_w - D_w}\right) \cdot 100 \quad (1)$$

$$\text{LFMC} = \left(\frac{F_w - D_w}{D_w}\right) \cdot 100 \quad (2)$$

where F_w is the fresh weight (i.e., weight prior to rehydration), D_w is the dry weight and T_w is the turgid (or saturated) weight of the fuel (that is, leaf or shoot).

Pressure–volume curves are typically derived from repeated measurements of Ψ_{leaf} and RWC on a cut leaf or shoot dehydrating on a bench. As leaves dehydrate, cell volume shrinks, turgor pressure decreases and osmotic potential (Ψ_π), and thus Ψ_{leaf}, decline [34]. The curve is obtained by plotting $-1/\Psi_{leaf}$ as a function of RWC (Figure 2a). Above the turgor loss point (Ψ_{TLP}), the curve is non-linear, but it approaches a linear relationship as $-1/\Psi_{leaf}$ falls below the Ψ_{TLP} [34]. This relationship can be reformulated to express LFMC as a function of Ψ_{leaf} by simply replacing RWC with LFMC as follows (Figure 2b):

$$\text{LFMC} = m_a \, \Psi_{leaf} + c_a \text{ for } \Psi_{leaf} > \Psi_{TLP} \quad (3)$$

$$\text{LFMC} = \left(\left(\frac{-1}{\Psi_{leaf}}\right) - c_b\right) / m_b \text{ for } \Psi_{leaf} < \Psi_{TLP} \quad (4)$$

where m_a and c_a are the slope and intercept for the linear model of LFMC and Ψ_{leaf} above the Ψ_{TLP}, and m_b and c_b are regression coefficients for the non-linear model of LFMC and $-1/\Psi_{leaf}$ below the Ψ_{TLP},

respectively. Note, m_b and c_b can be calculated from a linear regression if Equation (4) is rearranged to model $-1/\Psi_{leaf}$ as a function of LFMC. Equations (3) and (4) will have the exact same form whether RWC or LFMC are used as the dependent variable, assuming there are no changes in leaf dry matter content (see Section 6).

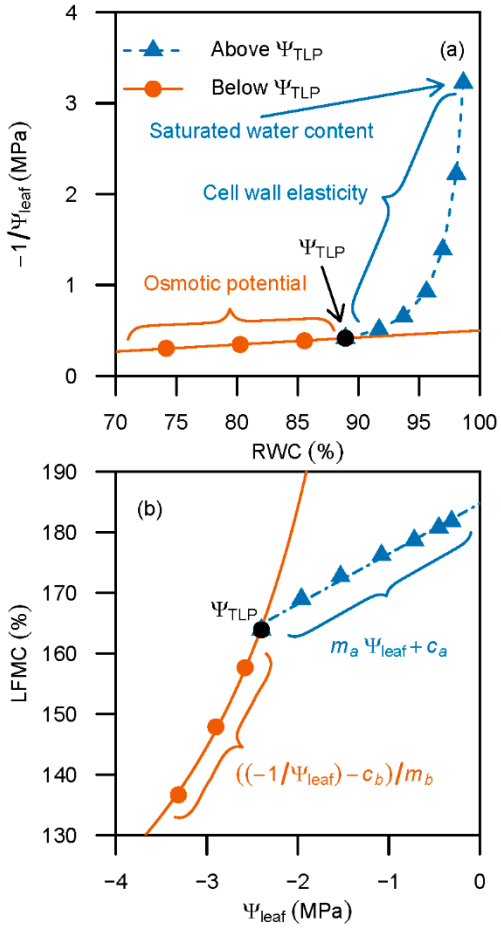

Figure 2. (**a**) Pressure–volume curve illustrating the non-linear relationship between $-1/\Psi_{leaf}$ and declining water status (RWC) (when $\Psi_{leaf} > \Psi_{TLP}$), and the linear relationship (when $\Psi_{leaf} < \Psi_{TLP}$). Additionally shown is the turgor loss point (Ψ_{TLP}), saturated water content, and region of the graph affected by cell wall elasticity and osmotic potential at full hydration. (**b**) Relationship between live fuel moisture content (LFMC) and Ψ_{leaf} above and below the Ψ_{TLP}, derived from pressure-volume curve relationships. Note, this is a theoretical relationship and not based on observations.

To date, there have been few studies modelling LFMC as a function of Ψ_{leaf} (but see [19,22]). Here, we use data from our case study (see Section 3) to demonstrate that declining LFMC during drought can be modelled from Ψ_{leaf} using Equations (3) and (4). Note, our data represent progressive measurements on multiple leaves during drought, rather than on a single leaf dehydrating on a bench. We modelled the decline in LFMC and Ψ_{leaf} using Equation (3) (for data > Ψ_{TLP}) and Equation (4) (for data < Ψ_{TLP}: $-1/\Psi_{leaf}$ versus LFMC). The transition between the two models (the Ψ_{TLP}) was estimated following Sack et al. [41], whereby the r^2 of the linear regression below the Ψ_{TLP} was maximised. The Ψ_{TLP} calculated in this way was similar to that calculated from traditional pressure-volume curves using excised leaves dehydrating on a bench (the mean absolute error was 0.19 MPa, Figure S2 in Supplementary Material).

For each of our eight species of eucalypt, we found that the model below the Ψ_{TLP} (i.e., Equation (4)) fit the data well: r^2 = 0.77–0.94, $p < 0.001$ (Figure 3). Above the Ψ_{TLP}, the regression slope was close to zero for many species, and so the fit of the linear models (i.e., Equation (3)) was relatively poor, as expected when regression slopes are at or near zero: $p > 0.05$ for five spp. and $p < 0.05$ for three spp.

(r^2 = 0.33–0.44 for these spp.). However, the intercepts were always statistically significantly different from zero ($p < 0.001$). Despite the poor fit of the linear regression above the Ψ_{TLP} for some species, we think a linear model is still the best model to fit, since (a) there is a good theoretical basis for doing so [34]; and (b) the data do not exhibit a non-linear relationship. As discussed later in Section 7.2, modelling LFMC above ~150–200%, which is above the value of LFMC at the Ψ_{TLP} for these species, is of relatively minor importance for predicting critical periods of live fuel moisture content, as most wildfires occur well below this value.

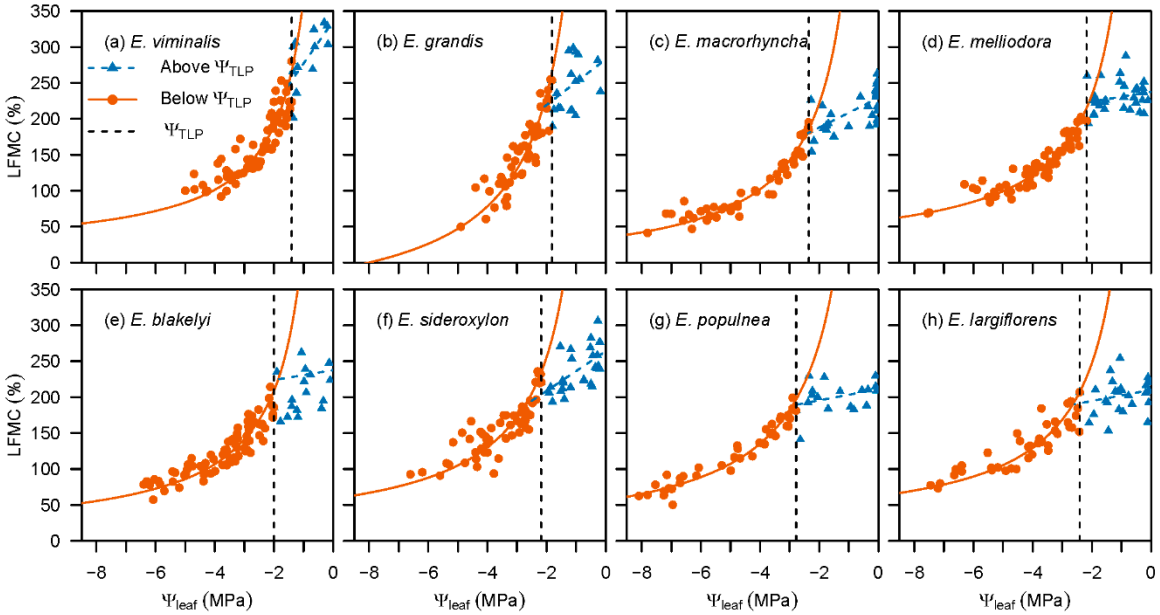

Figure 3. Decline in LFMC and Ψ_{leaf} modelled using Equation (3) (for data > Ψ_{TLP}) and Equation (4) (for data < Ψ_{TLP}: $-1/\Psi_{leaf}$ versus LFMC), for saplings of eight *Eucalyptus* species. Species are ordered by increasing moisture index (ratio of precipitation to potential evapotranspiration) from climate of origin, i.e., *E. largiflorens* is from the most arid climate. Regressions for all species were statistically significant ($p < 0.05$), except the slope of the linear regression above the Ψ_{TLP} for the following species: *E. grandis*, *E. melliodora*, *E. blakelyi*, *E. populnea* and *E. largiflorens*. (**a**) *E. viminalis*; (**b**) *E. grandis*; (**c**) *E. macrorhyncha*; (**d**) *E. melliodora*; (**e**) *E. blakelyi*; (**f**) *E. sideroxylon*; (**g**) *E. populnea*; (**h**) *E. largiflorens*.

This case study demonstrates that LFMC can be modelled as a function of Ψ_{leaf} following the pressure–volume curve approach. There is an extensive literature that quantifies pressure–volume curve parameters, globally [40]. Utilising this literature to model LFMC offers the potential to rapidly develop models for the prediction of spatiotemporal change in LFMC across a range of ecosystems. While Ψ_{leaf} does not directly affect LFMC (rather, it is foliar water content that affects Ψ_{leaf}), developing a model of LFMC as a function of Ψ_{leaf} provides a framework for modelling LFMC from soil water content, which is discussed in the next section.

5. How Drought Models Can Inform Fire Models: Predicting Live Fuel Moisture Content

Leaf water potential is a key parameter for modelling carbon and water fluxes [42] and is now being implemented into land surface models [43]. These models have largely been developed to predict changes in carbon and water cycling due to drought but could be harnessed to predict live fuel moisture content. Figure 4 outlines the general framework for how Ψ_{leaf}, and subsequently LFMC, can be modelled from soil water content.

Plant water potential generally equilibrates with root-zone soil water potential (Ψ_{soil}) overnight [44]. For this reason, pre-dawn Ψ_{leaf} is frequently used as a proxy for Ψ_{soil}. Soil water potential can in turn be modelled from soil water content and basic soil hydraulic properties that govern the soil water retention

curve, such as soil texture (see [42]). We note that in some circumstances, night-time transpiration, solute accumulation and other processes may affect the relationship between pre-dawn soil and leaf water potential [45]. Diurnal values of Ψ_{leaf} will fluctuate relative to Ψ_{soil} due to transpiration [42]. These Ψ_{leaf} fluctuations can be modelled from a soil-plant-atmosphere-continuum type of model. For example, Tuzet et al. [42] developed a coupled model of stomatal conductance, photosynthesis and transpiration that predicts diurnal values of Ψ_{leaf}. Required inputs for this model are Ψ_{soil}, vegetation attributes that control hydraulic conductance (leaf area index, canopy height, plant hydraulic resistance, canopy mixing length), stomatal conductance and atmospheric demand for water (Figure 4). A similar approach has been proposed for modelling LFMC of *Calluna*-dominated heathlands in the United Kingdom [46].

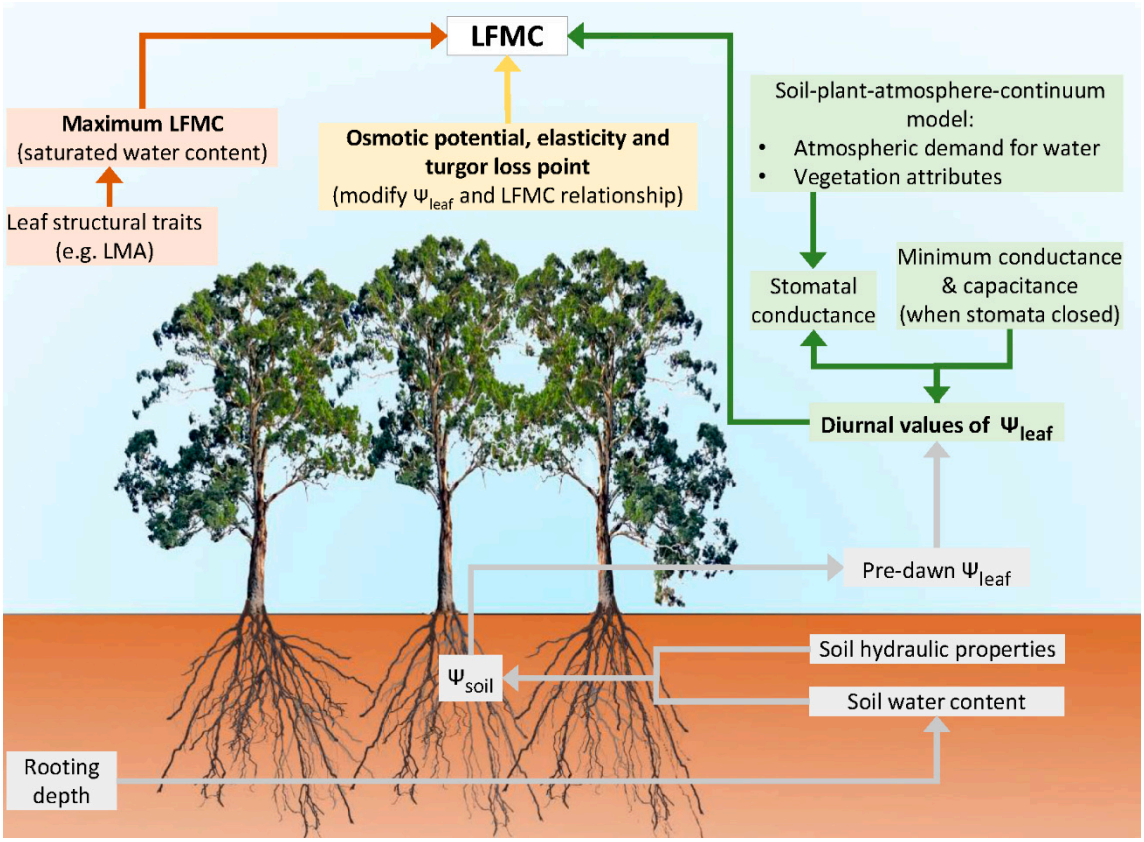

Figure 4. Overview of plant structural and physiological traits which modify the relationship between live fuel moisture content (LFMC) and soil water content.

While diurnal variation in LFMC is largely a function of the stomatal regulation of water loss, water loss still occurs following stomatal closure through the cuticle and incompletely closed stomata [47]. Thus, diurnal values of Ψ_{leaf} will be dependent on rates of minimum conductance following stomatal closure, which is particularly relevant during drought. However, the processes controlling leaf desiccation in very dry soil are poorly understood compared to the stomatal regulation of Ψ_{leaf} [18], and thus are a critical knowledge gap for modelling both drought vulnerability and diurnal LFMC under extreme drought conditions.

6. Drought-Related Plant Traits Determine the Response of Live Fuel Moisture Content to Drying Soil

Drought-related plant traits, such as rooting depth and the leaf traits which modify the relationship between RWC and Ψ_{leaf}, affect the development of critically low values of LFMC (Figure 2a).

Thus, existing models for the prediction of live fuel moisture content models may be improved by incorporating these traits (Figure 4). There is already recognition that plant traits play a role in forest flammability. For example, leaf size and shape affect the packing of litter beds, which in turn affects ignitability (i.e., ease of ignition; [36,48]). Similarly, leaf mass per area of live foliage affects ignitability [49,50]. We now discuss the role of plant traits in determining LFMC dynamics.

Rooting depth determines access to water resources, and will therefore influence seasonal and inter-annual LFMC dynamics. For example, in Mediterranean environments, tree species typically have access to deeper soil water or ground water reserves than co-occurring shrubs, and consequently exhibit less seasonal variation in LFMC [19,51]. In addition to lifeform, rooting depth is often related to post-fire regeneration strategy. For example, species that can resprout following high intensity fire typically have greater allocation to roots and deeper root systems than species lacking this capacity, and consequently exhibit less seasonal variation in LFMC than non-resprouting species [19,24].

One of the central leaf traits characterising physiological responses to soil dryness is the turgor loss point (Ψ_{TLP}), which defines the operating range of water potentials that plants use to control moisture content [52]. Above the Ψ_{TLP} the rate of decline of Ψ_{leaf} with RWC is largely dependent on cell wall elasticity [34]. Below the Ψ_{TLP}, cell walls are relaxed and the rate of decline in Ψ_{leaf} with RWC is dependent upon the concentration of solutes in cells, which is characterised by osmotic potential. While the Ψ_{TLP}, cell-wall elasticity and osmotic potential at full turgor control the rate of decline in LFMC with Ψ_{leaf}, saturated water content affects the absolute value of LFMC. Saturated water content is analogous to maximum LFMC and is negatively correlated with leaf structural properties, including leaf mass per area (LMA), leaf thickness and leaf density [35]. Here, we found that maximum LFMC from each of the eight *Eucalyptus* species in the common garden study declined with increasing LMA (Figure 5a). This relationship between LFMC and LMA is expected, since both traits incorporate leaf dry mass, and will therefore be auto-correlated. Thus, the key leaf traits that determine variation in the relationship between soil water content and LFMC are the Ψ_{TLP}, LMA, leaf elasticity and osmotic potential at full hydration.

These plant traits are known to vary along environmental gradients. The Ψ_{TLP}, leaf cell wall elasticity and osmotic potential at full hydration all generally decline with site water availability, enabling plants to continue gas exchange during periods of soil water deficit [40]. Our case study results are largely consistent with this observation. We examined the relationship between leaf traits and the climatic moisture index of the location of origin of each species (obtained from the Atlas of Living Australia website at http://www.ala.org.au). We found that: (i) the Ψ_{TLP} increased with the climatic moisture index (Figure 5b); (ii) above the Ψ_{TLP}, the slope of Ψ_{leaf} versus LFMC (indicative of cell wall elasticity) increased with the moisture index (Figure 5c); and (iii) below the Ψ_{TLP}, the slope of $-1/\Psi_{leaf}$ versus LFMC (indicative of osmotic potential at full hydration) largely increased with the moisture index, although this correlation was not significant (Figure 5d). Plants can exhibit some plasticity in these traits through solute accumulation during drought or from wet to dry seasons [53]. Thus, there may be some variability in the relationship between LFMC and Ψ_{leaf} through time due to osmotic adjustment.

LMA also varies along environmental gradients, particularly light, temperature and nutrient and water availability [54]. Here, we found that LMA from our case study *Eucalyptus* species increased with declining moisture availability from their climate of origin (Figure 5e). LMA also increases during leaf maturation [55]. This effect of leaf age has been associated with seasonal declines in conifer LFMC [56]. Therefore, we suggest that LFMC models may be improved by taking seasonal variation in LMA into account.

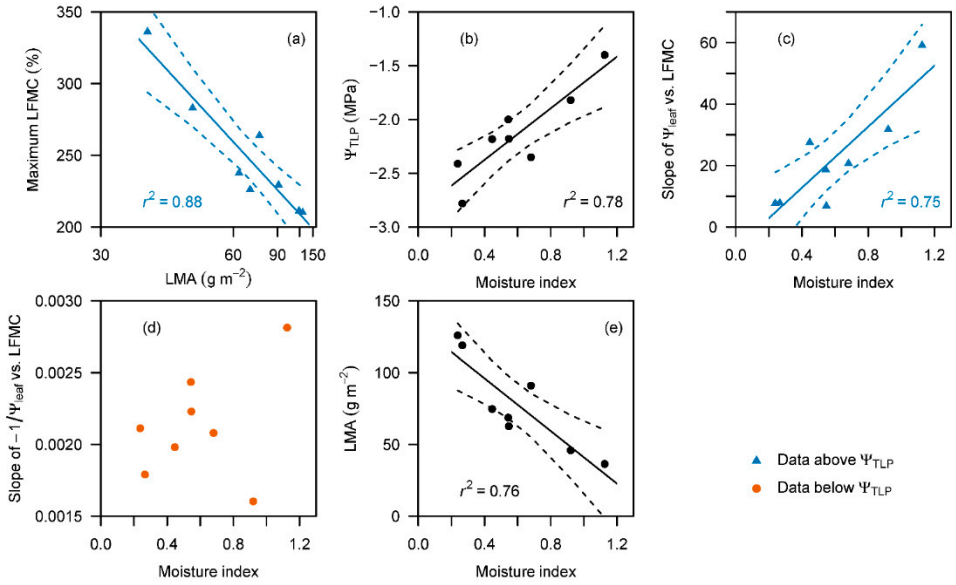

Figure 5. Relationship between (**a**) maximum live fuel moisture content (LFMC) and average leaf mass per area (LMA) in eight *Eucalyptus* species in a common garden experiment; and (**b**–**e**) plant ecophysiological traits and the moisture index from the climate of origin (calculated as the ratio of precipitation to potential evapotranspiration), including (**b**) the turgor loss point (Ψ_{TLP}), (**c**) the slope of Ψ_{leaf} versus LFMC above the Ψ_{TLP} (analogous to cell wall elasticity), (**d**) the slope of $-1/\Psi_{leaf}$ versus LFMC below the Ψ_{TLP} (analogous to osmotic potential at full hydration), and (**e**) average LMA. Note, the same LMA values are used in (**a**,**e**), but the data are transformed by a negative reciprocal transformation in (**a**). Dashed lines represent the 95% confidence interval of each regression.

7. How Does Physiological Drought Stress Affect Fuel Availability

During the early stages of drought, declining soil water content will affect live fuel moisture content, as well as the moisture content of surface dead fuels. As the drought progresses, the onset of leaf shedding and, eventually, tree death will have major implications for fuel properties. Currently, there is a concerted research effort to quantify and predict thresholds in leaf- and branch-level die-back, and whole forest mortality [17,18]. However, linkages between thresholds in drought mortality and thresholds in wildfire risk have not been explicitly examined to date. Thus, joint research on drought and forest flammability presents a major opportunity to inform predictive models of wildfire risk. Thresholds in plant vulnerability to drought are typically calculated from leaf or xylem water potential [18] or drought indices [57], while thresholds in wildfire risk are typically calculated from observed relationships between the area burnt by wildfire and fuel moisture content across large spatial areas (e.g., [9,58]).

7.1. Influence of Physiological Drought Stress on the Distribution of Dead Fuels

Plant vulnerability to cavitation is a major predictor of drought-induced mortality [18], and is therefore likely to affect the amount and spatial distribution of dead fuels within a forest. When cavitation is severe enough to trigger leaf death, it results in the transformation of live fuels into dead fuels. While they are retained within the canopy, these dead fuels decline to moisture contents well below those of live fuels. These senescent canopy fuels may therefore increase the probability of crown fire [3,10,36]. When these dead fuels are shed from the canopy, there is an influx of litter to the surface fuel bed. Initially, these litter fuels are likely to be relatively uncompacted, and thus well-aerated and available to burn [36]. Thus, leaf shedding may potentially increase the likelihood of surface fires, although the likelihood of crown fires may decrease due to the lowered overall fuel load within the tree canopy. Thus, we hypothesise that physiological drought stress can lead to an increase in the probability of large forest fires.

There is some evidence for this hypothesis. For example, leaf shedding is known to occur during infrequent drought events in eucalypt forests [59,60], and this coincides with periods of peak wildfire activity in these forests ([14]; Figure 6a). Similarly, in Amazonian forests, leaf shedding during severe drought events coincides with increased fire activity [61]. There is also some evidence that leaf death and subsequent shedding due to causes other than drought-induced cavitation can affect flammability. For example, in Mediterranean *Pinus halepensis* stands, needle senescence occurs during late June and mid-July, which coincides with peak fire activity in the region ([3]; Figure 6b). In contrast, in western North America, defoliation due to bark beetles does not result in an increase in the area burnt by wildfire [62], and may even reduce fire severity (i.e., fuel consumed) due to decreased canopy fuel loads [63]. Further, while seasonal leaf senescence may coincide with peak fire activity in many regions, this is not necessarily evidence that physiological drought stress is a causal factor of wildfires. Rather, physiological drought stress may simply be correlated with the causal factors of fire intensity, such as high atmospheric evaporative demand.

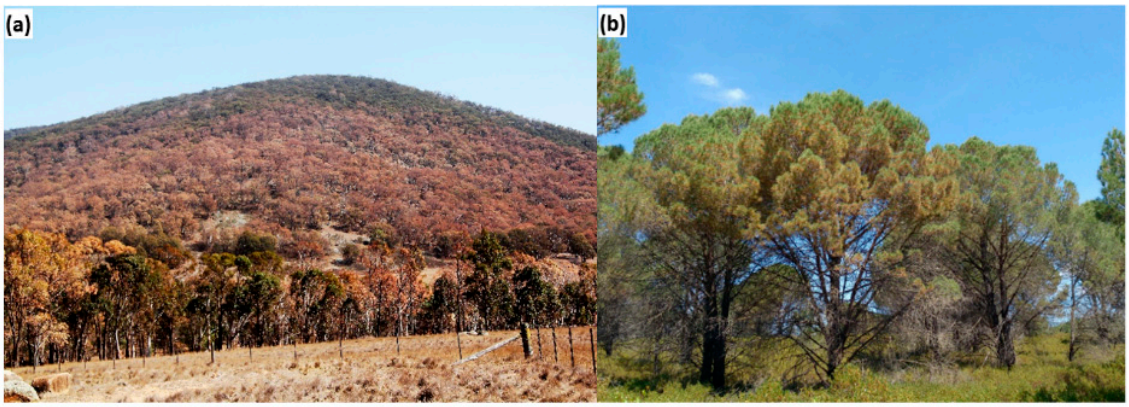

Figure 6. (**a**) Eucalypt woodland in north-eastern New South Wales, Australia, during severe drought in October 2019, illustrating the conversion of live fuels (i.e., foliage) into dead fuels. In this region, over five million hectares was subject to wildfire in 2019/2020. (**b**) Seasonal needle senescence in *Pinus halepensis* in Catalonia, Spain. Several days following this photo (22 June 2019), large fires occurred nearby. Image credit: Carles Arteaga.

7.2. Co-Occurrence of Thresholds in Physiological Drought Stress and Wildfire

Thresholds in drought vulnerability vary substantially among species, which may manifest in different thresholds in wildfire risk across biomes. The potential linkages between thresholds in drought vulnerability and wildfire risk have so far not been explicitly examined. A key barrier to investigating this linkage is the differing metrics and terminology used in the drought and fire research disciplines, e.g., RWC and LFMC. By developing a model of LFMC based on Ψ_{leaf}, we can overcome this barrier, and begin examining whether drought and fire thresholds co-occur. Examining the relationship between physiological drought stress and wildfire may potentially lead to new insights and hypotheses about the mechanisms underlying fire occurrence, and development of more reliable tools for predicting the risk of large wildfires.

Several studies have demonstrated that when fuel moisture content declines below a threshold value, there is a significant increase in the area burnt by wildfire. For live fuels, thresholds of 70–95% have been identified for Mediterranean shrublands [58,64,65] and 100–120% for forests [9,66]. We note that a recent discussion has emerged in the literature on the methods used to estimate these critical LFMC thresholds, with alternate methods likely to result in small changes in these threshold values (e.g., a ~10% difference in thresholds was observed in Mediterranean shrublands, depending on the method applied; [65]).

Using our common garden case study, we were able to calculate the value of LFMC when the eucalypt saplings were experiencing drought stress, and compare these values of LFMC with critical thresholds of LFMC identified for landscape-scale fires in eucalypt forests and woodlands across south-eastern Australia [9]. We calculated the value of LFMC at three metrics of physiological drought stress: (i) leaf P_{50}, which is a measure of the Ψ_{leaf} corresponding to a 50% decline in maximum leaf hydraulic conductance, and is commonly used to compare leaf hydraulic vulnerability among species [67]; (ii) leaf P_{88}, which is a measure of the Ψ_{leaf} corresponding to an 88% decline in maximum leaf hydraulic conductance and may better represent critical hydraulic failure [68]; and (iii) the value of LFMC associated with the initiation of leaf shedding (defined here as 10% of total canopy leaf shedding, see Section 3). We found that the value of LFMC at leaf P_{50} was largely above the critical threshold of ~102% identified for landscape-scale fire in eucalypt forests and woodlands ([9]; 91–120%, Figure 7a). However, the value of LFMC at leaf P_{88} was at or below this critical threshold (77–102%; Figure 7b). We also found that for all except the most mesic species, the LFMC value corresponding to the initiation of leaf shedding was at or below this same critical threshold of 102% (Figure 5c).

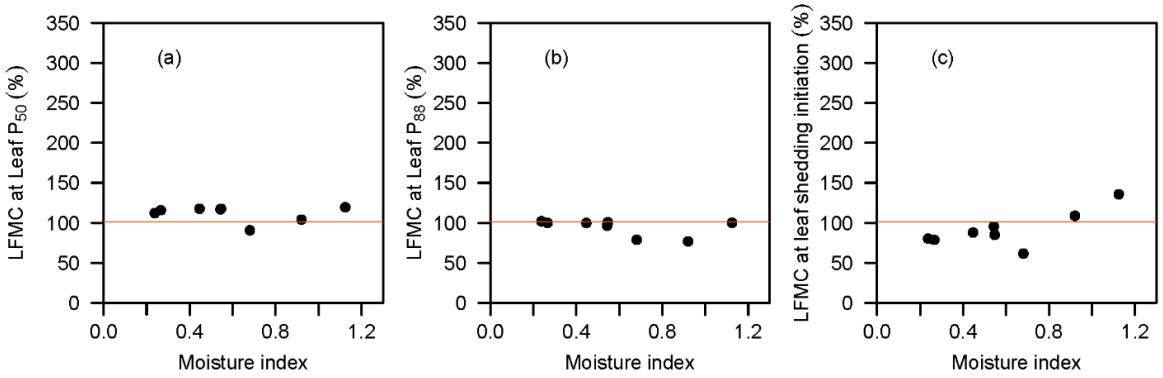

Figure 7. Value of LFMC at (**a**) leaf P_{50}, (**b**) leaf P_{88} and (**c**) initiation of leaf shedding (when up to 10% leaf shedding had occurred) for eight species of *Eucalyptus*. The *y*-axis range is the same as for Figure 3, to illustrate the range of LFMC values observed in the case study. The horizontal lines represent the LFMC threshold (~102%) associated with a step-change in fire activity for south-eastern Australian eucalypt forests and woodlands (see [9]).

It is remarkable that the value of LFMC at critical periods of drought stress in eucalypt saplings aligns so closely with the critical LFMC threshold, leading to a step-change in the area burnt by wildfire across south-eastern Australian forests and woodlands. These results support our hypothesis that physiological drought stress contributes to an increased probability of large forest fires. We note that other factors are important in contributing to these LFMC thresholds, in particular the increasing connectivity between patches of dry fuel that occurs across the landscape as LFMC declines, e.g., the drying of gullies which would otherwise act as a fire break [69].

8. Bridging the Gap between the Drought and Fire Literature

We have demonstrated that plant responses to drought affect fuel attributes, and thus may exert an important influence on the probability of wildfire. The establishment of better links between ecophysiological and fire behaviour research communities has the potential to transform knowledge of fire dynamics. We propose three major research directions:

1. Build connections between the drought and fire literature, in particular, identify ways to translate between the different measures used in each, e.g., relative water content and live fuel moisture content.
2. Utilise ecophysiological principles and metrics of drought vulnerability to develop new, predictive models of fuel dynamics.

3. Investigate the application of physiological knowledge of critical properties of plants for fire behaviour modelling.

The potential applications of this proposed research include (i) the development of new types of live fuel moisture content models which do not require species-specific calibrations; (ii) the capacity to model live fuel moisture content under future climatic conditions; (iii) the potential to derive new insights into the mechanisms underlying major wildfire events; and (iv) the development of physiologically based thresholds of forest flammability.

There is a large body of literature quantifying pressure–volume curve parameters (e.g., turgor loss point, osmotic potential and elasticity) globally [40]. Applying this research to model LFMC as a function of Ψ_{leaf} requires conversion from RWC to LFMC. One method to convert between RWC and LFMC is to develop a model of maximum LFMC, i.e., when RWC is 100%. The value of LFMC at critical values of RWC can then be readily calculated. For example, the value of RWC at the turgor loss point is commonly calculated in pressure–volume curves, and can be easily converted to LFMC if the maximum LFMC is known for a given species. Given that maximum LFMC is auto-correlated with LMA (see Section 6), and LMA is a common and easily measurable trait [54], quantifying the relationship between maximum LFMC and LMA would provide a pathway to rapidly convert between RWC and LFMC across many species globally. Thus, research on the leaf structural and environmental drivers of maximum LFMC is required to bridge the gap between the drought and fire literature.

While we have established that there is a connection between plant responses to drought and forest flammability, applying this research to fire behaviour modelling requires spatially explicit models of relevant plant traits, to model plant responses to variation in soil water content, which is not trivial. An important challenge to developing a physiologically based model of LFMC as a function of soil water content will be characterising rooting depth. In particular, characterising whether species have access to groundwater resources, which can buffer LFMC against seasonal variation in soil moisture content [19]. Vegetation access to groundwater can be inferred from remotely sensed observations of canopy greenness and surface temperature [70]. Characterising access to water resources among co-occurring species may be inferred from plant function types, e.g., trees versus shrubs, or post-fire resprouting versus non-resprouting species. We suggest further studies to test the generality of these relationships between plant functional types, access to water resources and seasonal variability in LFMC dynamics across biomes.

A further challenge will be modelling the leaf-level traits which govern responses to declining soil water content. We suggest modelling the key leaf-level traits as a function of environmental gradients, in particular aridity and soil nutrient content. However, many of these traits can vary seasonally and inter-annually, as a function of phenology or climate. For the purposes of modelling wildfire risk, these seasonal dynamics in leaf traits may be somewhat unimportant, given that wildfires typically only occur during particular seasons. Thus, research efforts to quantify these plant traits should prioritise measurements during the fire season.

We hypothesise that leaf death and subsequent shedding as a result of drought-induced cavitation may affect fire behaviour in multiple, opposing directions. Clearly, this hypothesis requires further research, and would benefit greatly from quantification of the extent and timing of leaf death and subsequent shedding. It has been hypothesised that leaf death due to drought occurs as a protective mechanism to delay dangerous cavitation within stems; however, this is not consistent among species [71]. Furthermore, the environmental cues that trigger seasonal leaf death and shedding have often not been well characterised. Thus, further studies on the mechanisms underlying leaf death, in addition to observations on the extent of leaf death and shedding during drought are suggested.

Further studies are also required to assess the linkages between physiological drought stress and wildfire occurrence. We suggest additional research focuses on quantifying the distribution of LFMC at critical periods of drought stress (i.e., critical thresholds of leaf/stem cavitation), and comparing these values with observed LFMC thresholds that lead to a step change in area burnt by wildfire. Establishing a physiological basis for thresholds in wildfire occurrence would enable the quantification and

prediction of wildfire risk across biomes, without the need for local empirical modelling. Investigation of the relationship between physiological drought stress and wildfire occurrence may also be facilitated by remotely sensed metrics of vegetation water stress. An indicator of vegetation water stress is when evapotranspiration declines below seasonal averages [72]. Recent advances in remote sensing have enabled estimation of evapotranspiration over large spatial scales at high spatial resolution [73]. Linking remotely sensed evapotranspiration with drought metrics derived from precipitation and potential evapotranspiration would enable large-scale investigation of the relationships between vegetation drought stress and wildfire activity.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/11/7/779/s1, Figure S1: Scanned images of the leaves of each species used in the common garden study. Not to scale.; Figure S2: Turgor loss point (Ψ_{TLP} ± 1SE) of eight *Eucalyptus* species, calculated from standard pressure-volume curves (bench dehydration method) and Ψ_{TLP} calculated from progressive observations of leaf water potential (Ψ_{leaf}) and live fuel moisture content (LFMC) of plants subject to imposed drought. Mean absolute error is 0.19 MPa.

Author Contributions: R.H.N., C.J.B., V.R.d.D., B.C., B.E.M., R.A.B. and M.M.B. developed the ideas, C.J.M. and X.L. contributed the case study data. R.H.N. wrote the manuscript. All authors have read and agree to the published version of the manuscript.

Funding: We thank the New South Wales Government's Department of Planning, Industry and Environment for providing funds to support this research via the NSW Bushfire Risk Management Research Hub; the Spanish Government (RYC-2012-10970, AGL2015-69151-R); an Australian Research Council Linkage grant with the New South Wales Department of Planning, Industry and Environment (LP140100232); and an Australian Research Council Future Fellowship (FT130101115).

Conflicts of Interest: The authors declare no conflict of interest.

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